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Invasive plant species and soil microbial response to wildfire burn severity in the Cascade Range of Oregon

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ABSTRACT

Exposure of soil to severe heating during a wildfire volatilizes soil nutrients and causes mortality of microbial communities, potentially facilitating invasion by non-native plant species. In this study, we investigated the chemical and biotic factors associated with severely burned "red" soil and less severely burned "black" soil from a recently burned forest on the eastern slope of the Cascade Range in Oregon. Specifically, we examined the effects of burn severity on plant growth, AM fungal colonization and soil microbial communities as indicated by PLFA (phospholipid fatty acid) analysis. Soil nutrients, arbuscular mycorrhizal (AM) fungi, microbial abundance and plant growth were all significantly reduced in red soils. Native and non-native plants exhibited differential growth in red and black soil, with non-natives growing more rapidly. Despite this rapid growth, non-native plant biomass was significantly lower in red soil, whereas native plant biomass did not differ between red and black soils. These findings suggest that some native species may out-compete non-native species in low-resource environments, such as severely burned red soil, where organic matter, soil nutrients and soil microbes are reduced by severe soil heating.
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1. Introduction

Fire is a key disturbance process in most ecosystems. Low temperature fire plays an important role in maintaining forest ecosystems by removing dead and accumulated vegetation and quickly releasing nutrients bound in litter, thus enriching the soil. The accumulation of fuels after decades of fire suppression, in addition to a combination of other factors, has contributed to more frequent high-severity, stand-replacing wildfire events in the western United States. With this increase in the last decade, forest researchers have become interested in the effects of fire severity on forest ecosystem resources, including soil organic matter, soil nutrients, and soil biota (Cromack et al., 2000). Fire burn severity is a qualitative measure that refers to the overall effect of fire on an ecosystem (Neary et al., 1999). It relates to the effect of fire on soil and site resources that control ecosystem sustainability (Neary et al., 1999). The component of fire severity that results in the greatest belowground damage to ecosystems is duration of combustion (Neary et al., 1999).

Small areas of soil associated with the complete combustion of large pieces of decaying wood or stumps in direct contact with the soil can be found scattered throughout burned areas. These severely burned soils show a distinctive color change where the top layer of mineral soil changes to various shades of red due to excessive heating and oxidation of the soil matrix. These severely burned, reddened sites are commonly found as long, narrow, linear strips ranging from 0.6 to 3 m or more long, and 5 to 35 cm wide that were created as decaying logs were consumed by fire. They also can be found as deep, irregular patches often 90 cm or more in diameter, where stumps and root systems were consumed by fire (Shank, 2004). In our study area, red soils were observed on 3–19% of the forest floor, with higher percentages in areas that contained large down wood from previous fires (Shank, 2004). Smoldering conditions that create red soils volatilize soil nutrients, reducing nutrient availability and plant growth in the short or long term (Neary et al., 1999). No research, to our knowledge, has been conducted on soil chemistry and soil microbial and plant communities in naturally occurring wildfire-induced red soils. However, the effects on soil and vegetative properties from scars left after burning large slash piles (Korb et al., 2004) provides some insight into severely burned soil conditions. Severe soil burning not only causes mortality of most soil organisms and plant roots, thereby changing nutrient cycling patterns, but also alters soil chemical and physical properties, such as the structure, porosity, infiltration and water storage of the soil (Neary et al., 1999), and increases the presence of "weedy" plant species (Goodwin and Sheley, 2001).

Disturbance from wildfire modifies ecosystem processes and favors early successional plant species. Due to their aggressive nature, many non-native invasive plants exploit the initial decreases

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in competition (Harrod and Reichard, 2001) and the flush of nutrients after fire (Certini, 2005), essentially out-competing many native early seral plants, thus altering soil nutrient dynamics and microbial communities in the soil (Harrod and Reichard, 2001). Fires, rarely burning uniformly through an area, usually create mosaics of varying burn severity across a post-fire landscape (Agee, 1998). Although many studies illustrate how fire facilitates the establishment of invasive non-native plant species (Vitousek et al., 1996; Harrod and Reichard, 2001; Korb et al., 2004), the role of variable burn severity on the introduction and establishment of non-native plants remains unclear (Parks et al., 2005).

Recent studies showing altered soil microbial community composition in conjunction with the invasion of non-native plant species (Kourtev et al., 2002; Wardle et al., 2004; Wolfe and Klironomos, 2005; Hawkes et al., 2006), as well as changes in soil properties (Ehrenfeld, 2003), emphasize that exotic invasions have profound and unpredictable effects on ecosystem processes and soil microbial communities. Research suggests arbuscular mycorrhizal (AM) fungi can contribute to the maintenance of and diversity within plant communities (van der Heijden et al., 1998b; Klironomos et al., 2000; Bever, 2002; Stampe and Daehler, 2003; Rillig, 2004). A series of studies by van der Heijden et al. (1998a,b) show that increasing AM fungal species richness promotes an increase in plant biodiversity, therefore directly influencing plant community structure and ecosystem productivity. With the abundance of AM fungi, as well as the chemistry of the soil being influenced by the severity of a disturbance (Korb et al., 2004), we hypothesize that a loss of microbial diversity and nutrient availability in areas of severely burned red soils will decrease plant diversity and ecosystem productivity in those areas.

This study examined the differences between paired severely burned red soil and less severely burned black soil. In particular, this study investigated the effects of soil burn severity on the growth of native and non-native plant species and the effect burn severity has on soil microbes as indicated by PLFA (phospholipid fatty acid) analysis. This research addressed several questions to compare soil burn severities: (1) are there differences in soil microbial community composition between burn severities? (2) Are there differences in soil chemistry between burn severities? (3) Are there growth differences between native and non-native plant species with respect to the soil burn severity in which they are grown? and (4) Are there differences in AM fungal colonization between native and non-native plant species with respect to the soil burn severity in which they are grown?

2. Methods

2.1. Study area

This study was conducted on the Booth and Bear Butte (B&B) Fire Complex on the eastern slope of the Cascade Range of Oregon in the Deschutes National Forest. The B&B Complex burned 36,733 ha in the summer of 2003. The area is characterized as a mixed conifer forest, dominated by ponderosa pine (*Pinus ponderosa* C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* Mirb., Franco.) with white-fir (*Abies concolor* Gord. & Glend., Lindl. Ex Hildebr.) or grand-fir (*Abies grandis* Dougl. ex D. Don, Lindl.) occurring as co-dominants (Simpson, 2007). On many sites, including the stands in our study, dense shrubs typify early successional stages after fires. An understory of snowbrush ceanothus (*Ceanothus velutinus* Dougl.), dwarf rose (*Rosa gymnocarpa* Nutt.), common snowberry (*Symphoricarpos albus* [L.] Blake), dwarf Oregon-grape (*Mahonia nervosa* [Pursh] Nutt.), trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and red huckleberry (*Vaccinium parvifolium* Sm.) occurs on our stands. Soils are Aquic Vitrixerands and Alfic Vitrixerands with sandy-loam texture. Elevations range from 1000 to 1300 m. Average temperatures range from −1 °C in the winter months to 20 °C in the summer months. Average annual precipitation ranges from 50 to 150 cm.

2.2. Field design and sampling

In August 2004, 1 yr post-fire, 10 sites (blocks) were randomly selected from 30 previously established areas containing red soil within the fire perimeter. Suitable sites contained enough red and black soil to allow for the removal of at least 6.5 kg of each soil type from the top 5 cm of soil. At each site, plots were established where severely burned red soil and adjacent, moderately burned black soil were collected (<1 m distance). Vegetation surveys were conducted on these plots the following summer.

Paired red and black soil samples (10 sites × 2 soil types = 20 total samples) were transported to the lab and stored up to 90 days at 4 °C until microcosm use. A subset of each soil sample was passed through a 2 mm sieve and sent to the Oregon State University Central Analytical Laboratory for chemical analysis. Soil samples were analyzed for: pH (Thomas, 1996); cation exchange capacity (CEC) ($cmol_c/kg$) (Sumner and Miller, 1996); plant available phosphorus (as Bray P) (ppm) (Kuo, 1996); available nitrate N (NO_3^--N) (ppm); initial extractable mineral N (NH_4^+-N) (ppm) (Hart et al., 1994); anaerobic incubation N (ppm); net mineralizable N (incubated N minus initial extractable NH_4-N) (ppm) (Bundy and Meisinger, 1994); total N (%) (Bremner, 1996); and total C (%) (Nelson and Sommers, 1996) using a LECO CNS 2000 Analyzer (LECO Corp., St. Joseph, MO). Twenty additional grams of each soil sample were sieved (<2 mm), immediately freeze-dried, and stored at −20 °C for phospholipid fatty acid (PLFA) analysis.

2.3. Growth room study

Three early successional native plant species occurring on the study sites were selected: the N-fixing perennial shrub *C. velutinus* (snowbrush) (Busse et al., 2007); the rhizomatous perennial *Epilobium angustifolium* (L.) (fireweed); and the perennial bunch grass *Elymus elymoides* (Raf.) Swezey (squirreltail). In addition, 3 aggressive, highly invasive non-native plant species of concern in the study area also were selected: the fast-growing annual grass, *Bromus tectorum* L. (cheatgrass); the dense-growing perennial bunchgrass, *Brachypodium sylvaticum* (Huds.) Beauv. (false brome); and the deep-rooted perennial forb, *Centaurea maculosa* Lam. (spotted knapweed). Seeds of most species were collected from the study region; seeds of *Brachypodium* were collected near Corvallis, Oregon.

Ceanothus seeds were scarified in 1 l of water at 95 °C, brought to room temperature, soaked in the water for 24 h, transferred to 8% water agar plates and stored in the dark at 4 °C for 90 days, then placed under wide spectrum fluorescent light at an average of 100 $\mu mol\ m^{-2}\ s^{-1}$ until germination. Seeds from all other species were surface sterilized with a 0.2% concentration of the DuPont manufactured fungicide Benlate® to prevent fungal inoculation, rinsed with distilled water and germinated on 8% sterile water agar plates. Seedlings of each species were removed from their seed coats and planted individually into 10 cm × 10 cm plastic pots filled with unsieved soil collected from the previously described site blocks (10 sites × 2 soil types × 6 species = 120 pots).

Seedlings were grown in a growth room under wide spectrum fluorescent light at an average of 150 $\mu mol\ m^{-2}\ s^{-1}$ with a 14 h light photoperiod and watered when necessary for 10 weeks. At harvest, a 20 g sample of soil from each pot was sieved (<2 mm) and immediately freeze-dried before being stored at −20 °C until PLFA analysis.

2.4. Shoot biomass and root colonization by AM fungi

Plant shoots were oven-dried at 37 °C for 12–14 days and weighed to measure within species differences in plant biomass between burn severities. Entire root systems were assessed for colonization of AM fungi and therefore, were not dried and weighed. Roots were cleared and stained using a modified Phillips and Hayman (1970) procedure to quantify AM fungal colonization.

Quantification of AM colonization was accomplished by direct estimation of the percentage of root length colonized by fungi (Biermann and Linderman, 1981), the most widely and currently used method of determining AM fungal colonization (Hart and Reader, 2002). Cleared and stained roots were placed in grid-lined petri dishes and inspected at 10–40× magnification with stereomicroscopy. More detailed observations were made by mounting root segments in lactoglycerol on microscope slides and examining at 100–400× magnification with compound microscopy. Total length of each root and total length of root colonization were estimated and expressed as a percentage of colonization by AM fungi (Rajapakse and Miller, 1992).

2.5. Vegetation survey

A vegetation survey was conducted on the 10 soil collection sites 2 yr post-fire in July, 2005. Percent cover by low herbaceous species was assessed according to a modified Quadrat-Charting Method (Mueller-Dombois and Ellenberg, 1974), using a m^2 frame and drawn to scale on a sheet of graph paper. The frame was set on top of each of the black and red soil sites and the percent vegetation cover was recorded, individual plants were identified to genus, and constancy (# plots on which a species was present × total $plots^{-1}$) was calculated for each species identified in each soil burn severity plot.

2.6. PLFA analysis

Phospholipids are fatty acids found only in living cell membranes which can be extracted from the soil to detect the presence and abundance of specific microbial groups. Phospholipid fatty acid (PLFA) analysis can detect changes in broad groups of soil organisms, such as bacterial and fungal groups, thus allowing for soil microbial community fingerprinting. A hybrid procedure of PLFA and fatty acid methyl ester (FAME) analysis as described in Fraterrigo et al. (2006), was used to characterize microbial community composition in the initial fresh and post-harvest soil samples. Microbial profiles were identified by analyzing the methyl-ester derivatives from the phospholipid extractions on a gas chromatograph (Hewlett-Packard 6890). It was equipped with a flame ionization detector and split/splitless inlet, and a 25 m × 0.2 mm inside diameter × 0.33 μm film thickness Ultra 2 (5%-phenyl, 95% methyl) capillary column (Agilent), using H_2 as the carrier gas, N_2 as the make-up gas, and air to support the flame. Gas chromatograph conditions were set by the MIDI Sherlock program (MIDI, Inc., Newark, DE, USA).

Peaks were identified with bacterial fatty acid standards and Sherlock peak identification software (MIDI, Inc., Newark, DE, USA). Fatty acids were quantified by comparing peak areas from the sample with peak areas of 2 internal standards, 9:0 (nonanoic methyl ester) and 19:0 (nonadeconoic methyl ester), of known concentration (Fraterrigo et al., 2006).

Total PLFA concentration (nmol PLFA g^{-1} soil) was used as an index of the total viable microbial biomass (Joergensen and Wichern, 2008). The sum of indicator fatty acids (expressed as mol %) was used as broad taxonomic microbial groupings (Table 1). Fungal to bacteria PLFA ratios also were used as a biomass index of the changes in the ratio of fungal to bacterial biomass as a function of burn severity (Bååth and Anderson, 2003).

Table 1
Indicator PLFAs and the corresponding microbial group for interpretation of PLFA community data.

Indicator PLFAs	Microbial group
*i*15:0, a15:0, *i*16:0, *i*17:0, a17:0	Gram-positive bacteria
16:1ω9*c*, 16:1ω7c, 17:1ω9*c*, 17:0 cy, 18:1ω7c, 19:0 cy	Gram-negative bacteria
10Me18:0, 10Me17:0, 10Me16:0	Actinomycetes
18:2ω6, 9*c*	Fungi
16:1ω5*c*	Arbuscular mycorrhizal (AM) fungi
20:4ω6 9, 12, 15*c*, 20:2ω6, 9*c*	Protozoan

3. Data analysis

3.1. Analysis of shoot growth, AM colonization, % cover and soil chemistry data

A randomized complete block design was used to test the response of individual plant species (3 native, 3 non-native) to growth in different burn severities. Paired *t*-tests were used to compare the differences in plant shoot growth and percent root colonization by AM fungi between paired red and black soil from 10 sites (blocks). *T*-tests were performed on 2 explanatory variables: soil burn severity type (red or black) and site. An arcsine square root transformation of the percent root colonization data was necessary to meet model assumptions. No other transformations of the data were necessary. Paired *t*-tests were also used to test the differences in soil chemistry and percent vegetation cover between red and black soil from the 10 sites.

Pearson correlations of plant shoot biomass grown in either red or black soil and soil chemical variables were computed. To reduce the effect of multicollinearity of the chemical variables in the model, we used a subset of non-correlated chemical variables, as determined by the correlation matrix (Zar, 2007): initial extractable NH_4, C, and P. For each plant species, biomass was regressed on initial extractable NH_4, C, P, the categorical variable fire severity, and all 2-way interactions of fire severity with the 3 chemical variables. Manual backward variable selection was used to select a more parsimonious model from this full model. All analyses were performed using S-Plus statistical software version 7.0 (Insightful Corporation, 1988–2005).

3.2. Analysis and ordination of PLFA data

All statistical analyses of PLFA data were performed using the PC-ORD version 5.0 software package (McCune and Mefford, 1999). PLFA data were relativized by sample unit totals to represent relative abundance (mol % of total PLFA) for each of the 36 identified PLFAs. Mol %, rather than absolute abundance, is most commonly reported and allows for comparisons of community structure without the effects of differences in microbial biomass or uncertain extraction efficiencies among samples.

Two matrices were used in the original fresh soil analysis: the species matrix (20 soil samples × 36 PLFAs) and a second matrix containing explanatory variables (20 soil samples × 17 variables). Two matrices also were used in the post-harvest soil analysis: the species matrix (114 soil samples × 36 PLFAs) and a second matrix containing explanatory variables (114 soil samples × 13 variables). Six out of 120 soil samples were unusable; therefore 114 samples were used in the PLFA analysis. Explanatory variables are listed in Table 2.

Table 2
Explanatory variables used in the second matrix for NMS ordinations. Note only the fresh soil matrix contained soil chemical variables: CEC, NO_3-N, NH_4-N, C and N. Similarly, only the post-harvest soil matrix contained 'species' variable.

Variable	Description
Groups	Categorical group indicators for sites, numbered 1–10
Severity	Binary indicator for "red" and "black" burn severity
Fungi	Sum of relative abundance of all fatty acids for fungi
AM fungi	Sum of relative abundance of fatty acids for AM fungi
Bacteria	Sum of relative abundances of all fatty acids for bacteria
G+ bacteria	Sum of relative abundance of all fatty acids for Gram-positive bacteria
G− bacteria	Sum of relative abundance of all fatty acids for Gram-negative bacteria
Actinomycetes	Sum of relative abundance of all fatty acids for actinomycete bacteria
Protozoa	Sum of relative abundance of all fatty acids for protozoa
F:B	Ratio of fungi to bacteria based on fatty acids listed above
PLFA	Sum of absolute abundance of all fatty acids
MSC	Sum of all misc. fatty acids not associated with any particular microbial group
Species	Categorical indicator for one of six plant species associations
CEC	Cation exchange capacity
NO_3-N	Amount of nitrogen comprised of nitrate
NH_4-N	Amount of nitrogen comprised of ammonium
C	Total carbon
N	Total nitrogen

Microbial community structure was examined using non-metric multidimensional scaling (NMS) with the Sørensen distance measure (Kruskal, 1964; Mather, 1976). Forty runs with real data were carried out and Monte Carlo simulations were conducted using 50 randomized runs and a stability criterion of 0.0001. The number of dimensions chosen in the model was assessed by comparing the NMS runs with the real data to Monte Carlo simulations with random numbers. The proportion of variation represented by each axis was assessed by calculating the coefficient of determination (r^2) between distances in the ordination space and Sørensen distances in the original distance matrix. The relationships between plots in ordination space and their corresponding environmental variables were assessed by overlaying the variables as a joint plot.

Blocked multi-response permutation procedure (MRBP) (Mielke, 1991) with Euclidean distance tested the null hypothesis of no difference in microbial community structure between burn severities across the 10 sites. Average distance function commensuration was incorporated in the MRBP to equalize the contribution of each variable to the distance function, in a sense relativizing the data (McCune and Grace, 2002). Median alignment also was incorporated to focus the analysis on within-block differences among treatments (McCune and Grace, 2002).

Pearson correlations of microbial abundance (total PLFA) within either of the two burn severities (red or black) and soil chemical variables were computed. To reduce the effect of multicollinearity of the chemical variables measured, models included a subset of chemical variables: initial extractable NH_4, C, P, and all interactions among factors. Multiple linear regression models were selected via manual backward variable selection using S-plus statistical software version 7.0 (Insightful Corporation, 1988–2005). All results were considered significant at a 0.05 alpha level.

4. Results

4.1. Soil microbial communities through PLFA analysis

Sums of PLFA signatures for all groups of microorganisms in freshly collected soil and soil harvested from pots after 10 weeks of growth (post-harvest soils) can be found in Tables 3 and 4, respectively. In the freshly collected soil, total microbial biomass, as represented by PLFA, was 60.9% lower in the red soil compared to black soil (Table 3). Relative abundance of most microbial groups found in red soil was significantly less than in black soil, while AM fungi and protozoan abundances as well as F:B ratios were not significantly different between the two burn severities. Post-harvest soils had less microbial biomass than fresh soil, but no other notable changes in microbial community structure were evident after growth of either native or non-native plant species (Table 4).

NMS of PLFA signatures of soil microbial communities from freshly collected red and black soil indicated that a two-dimensional solution best represented the data in reduced ordination space with final stress of 6.3 (Monte Carlo = 14.3, $P < 0.01$). After 87 iterations, the final configuration was deemed stable (final instability < 0.001). The NMS ordination showed significant separation between the microbial community structure with respect to burn severity (Fig. 1) (MRBP: $P < 0.01$; $A = 0.07$). No separation was apparent between soil collection sites (MRBP: $P = 0.23$, $A = 0.02$). Axis 1 corresponded with burn severity and showed a strong positive correlation with total nmol PLFA ($r = 0.695$), actinomycetes ($r = 0.845$), AMF ($r = 0.67$), and protozoa ($r = 0.553$), and had a strong negative correlation with total bacteria ($r = -0.854$) and Gram-negative bacteria ($r = -0.866$). Axis 2 showed weak correlations with all variables.

The NMS ordination of microbial community PLFA signatures from post-harvest soil indicated that a two-dimensional solution best represented the data in reduced ordination space with final stress of 11.3. After 152 iterations, the final configuration was deemed stable (final instability < 0.001). The NMS ordinations of post-harvest soil data displayed trends similar to those of the freshly collected soil data, with significant separation among the microbial community structure with respect to burn severity (MRPP: $P < 0.01$; $A = 0.11$) (Fig. 2). Unlike the ordinations of microbial community structure data from freshly collected soil, there was significant separation between the microbial communities with respect to plot (MRPP: $P < 0.01$, $A = 0.09$), as well as separation between the particular plant species (MRPP: $P = 0.04$; $A = 0.01$).

Multiple linear regressions revealed microbial biomass (measured by total nmol PLFA) had particularly strong relationships with soil C. Backward selection resulted in a significant model with soil burn severity and C ($n = 20$):

$$\text{PLFA} = 27.7(45.5) - 14.7(27.9) \times \text{severity} + 94.7(19.2) \times C, \quad R^2 = 0.84$$

4.2. Soil chemistry

All chemical analyses, with the exception of initial extractable NH_4-N, showed significant differences between the two burn severities (Table 5). Soil pH was highest in red soil, while soil P, NO_3-N, anaerobic incubation N, net mineralizable N, CEC, and total C and N all were highest in black soil. The severe loss of organic matter in red soil resulted in 71% less soil C than black soil, strongly contributing to the microbial community differences between red and black soil. Similarly, total N of red soils was 69% less in red soil than in black soil. These results are consistent with previous findings indicating that substantial changes in soil temperature during heating can result in volatilization of C and soil nutrients, mortality of soil microbes and shifts in species composition of survivors (Bååth et al., 1995; Pietikäinen et al., 2000; Knicker, 2007; Bormann et al., 2008).

4.3. Shoot growth

After approximately 10 weeks of growth, the average shoot biomass for each of the 3 non-native plant species, *Centaurea*,

Table 3
Sum of PLFAs given as both (Abs) absolute abundance (nmol PLFA g^{-1} soil) and (Rel) relative abundance (mol %) in freshly collected red and black soil at each site. Column headings are defined in Table 2. Bolded text indicates a significant difference between means ($\alpha = 0.05$, $n = 10$).

Site	Severity	PLFA	F:B ratio	Bacteria		G+ bacteria		G− bacteria		Fungi		AM fungi		Actino		Protozoa	
		Abs		Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel
UJ-1	Red	87.2	0.12	46.8	53.7	10.0	11.4	36.9	42.3	3.4	3.9	2.6	3.0	2.6	2.9	0.0	0.0
	Black	311.8	0.13	123.1	39.5	48.0	15.4	75.2	24.1	11.4	3.7	7.2	2.3	16.6	5.3	3.6	1.1
UJ-5	Red	55.9	0.25	28.1	50.3	3.3	6.0	24.8	44.3	6.2	11.0	1.3	2.3	1.7	3.1	1.2	2.1
	Black	437.7	0.12	133.9	30.6	43.2	9.9	90.8	20.7	8.3	1.9	10.5	2.4	26.6	6.1	10.0	2.3
LJ-7	Red	140.1	0.11	63.3	45.2	18.2	13.0	45.1	32.2	6.0	4.3	2.0	1.4	6.0	4.3	1.8	1.3
	Black	231.9	0.12	95.7	41.3	30.1	13.0	65.7	28.3	8.8	3.8	3.8	1.6	11.5	5.0	7.7	3.3
LJ-10	Red	282.1	0.16	78.0	27.7	27.1	9.6	50.9	18.0	22.3	7.9	26.1	9.3	20.9	7.4	30.0	10.6
	Black	377.4	0.29	145.8	38.6	53.4	14.2	92.3	24.5	10.6	2.8	4.9	1.3	16.5	4.4	18.3	4.9
LJ-12	Red	233.3	0.09	94.9	40.6	28.0	12.0	66.8	28.6	6.6	2.8	2.4	1.0	10.8	4.6	6.4	2.7
	Black	259.1	0.10	105.5	40.7	37.0	14.3	68.5	26.5	8.5	3.3	3.4	1.3	11.7	4.5	6.8	2.6
BH-1	Red	84.8	0.12	46.8	55.2	10.0	11.7	36.9	43.5	3.4	4.0	2.6	3.1	2.6	3.0	0.0	0.0
	Black	312.4	0.13	123.1	39.4	48.0	15.4	75.2	24.1	11.4	3.7	7.2	2.3	16.6	5.3	4.2	1.4
BH-6	Red	138.8	0.10	76.8	55.3	25.8	18.6	51.0	36.7	6.4	4.6	2.3	1.7	1.8	1.3	1.1	0.8
	Black	433.8	0.13	162.9	37.5	79.4	18.3	83.5	19.3	14.5	3.3	9.3	2.2	24.9	5.7	15.2	3.5
1210-3	Red	42.6	0.13	21.3	50.0	2.0	4.8	19.3	45.2	2.8	6.5	0.0	0.0	0.0	0.0	0.0	0.0
	Black	205.1	0.10	91.0	44.4	30.9	15.1	60.1	29.3	4.8	2.3	4.7	2.3	10.0	4.9	3.4	1.7
1210-6	Red	141.0	0.05	73.1	51.9	7.9	5.6	65.2	46.2	3.9	2.8	0.0	0.0	5.6	4.0	14.8	10.5
	Black	381.9	0.11	142.3	37.3	76.5	20.0	65.8	17.2	7.5	2.0	8.7	2.3	25.3	6.6	15.2	4.0
1280	Red	155.8	0.12	75.3	48.3	19.2	12.3	56.2	36.0	7.6	4.9	2.1	1.4	3.0	1.9	0.0	0.0
	Black	528.0	0.09	205.5	38.9	85.4	16.2	120	22.7	13.0	2.5	9.7	1.8	33.7	6.4	25.1	4.7
Mean (SE)	Red	**136.2** (23.9)	0.12 (0.02)	**60.4** (7.5)	**47.8** (2.7)	**15.1** (3.1)	**10.5** (1.3)	**45.3** (5.0)	**37.3** (2.8)	6.9 (1.8)	**5.3** (0.8)	4.1 (2.5)	2.3 (0.8)	**5.5** (2.0)	**3.2** (0.6)	5.5 (3.1)	2.3 (1.3)
	Black	**347.9** (32.4)	0.13 (0.02)	**132.9** (10.8)	**38.8** (1.2)	**53.2** (6.4)	**15.2** (0.9)	**79.7** (5.6)	**23.7** (1.2)	9.9 (0.9)	**2.9** (0.2)	6.9 (0.8)	2.0 (0.1)	**19.3** (2.5)	**5.4** (0.2)	10.9 (2.3)	2.9 (0.4)

Table 4
Sum of PLFAs given as both (Abs) absolute abundance (nmol PLFA g^{-1} soil) and (Rel) relative abundance (mol %) averaged from post-harvest red and black soil for each plant species grown. Column headings are defined in Table 2. SE denoted in parentheses ($n = 10$).

Species	Severity	PLFA	F:B ratio	Bacteria		G+ bacteria		G− bacteria		Fungi		AM fungi		Actinomycetes		Protozoa	
		Abs		Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel	Abs	Rel
Non-natives																	
CEMA	Red	97.2 (20.8)	0.16 (0.01)	44.0 (7.1)	49.8 (2.7)	11.3 (3.4)	9.8 (1.5)	32.7 (4.3)	40.0 (3.9)	5.5 (0.9)	6.7 (0.8)	1.9 (0.5)	2.0 (0.4)	3.9 (1.4)	2.8 (0.8)	1.2 (0.6)	0.7 (0.3)
	Black	300.3 (41.1)	0.20 (0.04)	109.0 (13.6)	37.5 (1.7)	39.5 (3.9)	13.9 (0.8)	69.5 (10.1)	23.6 (1.4)	6.9 (0.8)	2.4 (0.3)	18.1 (5.0)	5.7 (1.4)	17.3 (2.8)	5.8 (0.5)	7.7 (1.4)	2.6 (0.5)
BRSY	Red	65.2 (15.7)	0.18 (0.04)	29.5 (6.5)	48.2 (1.9)	7.3 (2.2)	11.6 (2.0)	22.2 (4.7)	36.6 (2.2)	4.1 (1.0)	6.9 (1.6)	1.6 (0.5)	1.9 (0.5)	2.7 (1.1)	3.1 (0.8)	0.9 (0.5)	0.7 (0.4)
	Black	213.4 (43.3)	0.24 (0.05)	74.6 (16.5)	34.0 (2.3)	32.1 (7.9)	13.9 (1.1)	42.5 (8.8)	20.1 (1.5)	6.9 (1.6)	3.3 (0.3)	11.1 (2.7)	5.4 (1.3)	11.7 (3.3)	4.7 (0.6)	8.7 (2.7)	4.2 (1.3)
BRTE	Red	97.5 (16.1)	0.16 (0.02)	46.6 (6.3)	50.8 (2.5)	12.2 (2.3)	12.5 (1.3)	34.4 (4.6)	38.3 (2.6)	5.8 (0.6)	6.7 (0.9)	1.9 (0.4)	1.7 (0.3)	3.9 (1.1)	3.4 (0.6)	1.0 (0.4)	0.8 (0.3)
	Black	245.2 (23.6)	0.14 (0.01)	95.4 (8.4)	39.5 (1.0)	40.5 (4.7)	16.1 (0.6)	54.9 (4.2)	23.4 (1.4)	9.3 (1.0)	4.0 (0.4)	5.2 (0.6)	2.2 (0.2)	13.0 (1.7)	5.1 (0.3)	5.9 (1.0)	2.4 (0.4)
Natives																	
ELEL	Red	115.2 (33.6)	0.22 (0.05)	46.3 (11.2)	43.6 (2.8)	15.9 (6.9)	11.1 (1.5)	30.4 (4.4)	32.5 (3.2)	6.2 (0.9)	7.4 (1.6)	4.9 (3.4)	2.4 (0.8)	7.8 (3.2)	6.0 (1.9)	1.8 (0.9)	1.1 (0.4)
	Black	212.0 (34.1)	0.15 (0.03)	78.7 (11.0)	39.2 (1.9)	32.3 (5.9)	14.9 (1.2)	46.5 (5.5)	24.3 (1.8)	7.7 (1.8)	3.9 (1.1)	6.1 (1.5)	2.6 (0.4)	13.9 (3.2)	5.8 (0.7)	7.6 (1.7)	3.9 (1.2)
EPAN	Red	125.3 (29.1)	0.21 (0.03)	49.8 (10.7)	42.3 (1.7)	14.8 (4.7)	9.1 (1.9)	35.0 (6.5)	33.3 (3.3)	8.9 (2.3)	8.5 (1.3)	2.1 (0.7)	1.3 (0.3)	6.3 (2.0)	3.8 (0.8)	3.2 (1.1)	1.9 (0.7)
	Black	277.6 (38.5)	0.17 (0.03)	94.5 (12.4)	34.2 (1.4)	36.8 (6.1)	12.4 (1.0)	57.8 (6.5)	21.8 (1.4)	13.4 (3.8)	4.5 (0.8)	6.7 (1.6)	2.2 (0.3)	15.9 (3.0)	5.5 (0.4)	9.6 (1.2)	3.6 (0.2)
CEVE	Red	112.5 (15.1)	0.13 (0.01)	52.1 (5.1)	48.2 (1.8)	15.9 (1.9)	14.4 (0.8)	36.2 (3.5)	33.8 (1.7)	5.6 (0.8)	5.3 (0.6)	1.9 (0.3)	1.6 (0.2)	4.9 (1.0)	4.1 (0.4)	1.3 (0.7)	0.9 (0.5)
	Black	287.7 (25.6)	0.12 (0.01)	112.8 (8.2)	39.8 (0.9)	51.7 (5.0)	17.8 (0.4)	61.1 (3.8)	22.0 (1.2)	7.8 (0.7)	2.9 (0.3)	7.2 (1.5)	2.4 (0.3)	17.7 (2.2)	6.0 (0.3)	8.2 (1.4)	2.7 (0.3)

Brachypodium, and *Bromus* had 85%, 73% and 33% less biomass, respectively, when grown in red soil (Fig. 3A). In contrast, shoot biomass of the three native plant species did not differ significantly between burn severities, although *Ceanothus* did have a non-

Fig. 1. NMS ordination of PLFA relative abundance by burn severity. Symbols represent the microbial community of freshly collected soil from each plot separated by burn severity. R^2 axis 1 = 0.84, axis 2 = 0.058. Vectors are based on summed abundances of specific PLFA groups and environmental variables. The length of the vector is proportional to the correlation between that variable and the NMS axis.

Fig. 2. NMS ordination of PLFA relative abundance by burn severity. Symbols represent the microbial community from red or black soil harvested from pots after 10 weeks of growth of individual native or non-native species grown in a growth chamber. R^2 axis 1 = 0.624, axis 2 = 0.272. Vectors are based on summed abundances of specific PLFA groups and environmental variables. The length of the vector is proportional to the correlation between that variable and the NMS axis.

Table 5
Paired *t*-test of differences in soil chemistry between two burn severities. Bolded text indicates a significant difference between means ($\alpha = 0.05$). SE denoted in parentheses ($n = 10$).

Response variable	Severity	Mean	t_9	*P*-value
pH	Red	7.9 (0.06)	5.18	<**0.001**
	Black	7.3 (0.08)		
Available P (ppm)	Red	3.5 (0.36)	−3.43	**0.007**
	Black	12.2 (2.5)		
Extractable NO_3-N (ppm)	Red	1.4 (0.36)	−2.48	**0.035**
	Black	4.3 (1.1)		
Initial extractable NH_4-N (ppm)	Red	36.7 (10.1)	−1.40	0.193
	Black	45.3 (10.6)		
Anaerobic incubation NH_4-N (ppm)	Red	44.5 (11.3)	−3.48	**0.006**
	Black	73.6 (12.5)		
Net mineralizable NH_4-N (ppm)	Red	7.7 (1.6)	−6.66	<**0.001**
	Black	28.3 (2.7)		
CEC ($cmol_c\ kg^{-1}$)	Red	9.4 (1.3)	−5.29	<**0.001**
	Black	18.3 (2.0)		
Total C (%)	Red	1.0 (0.16)	−8.16	<**0.001**
	Black	3.5 (0.29)		
Total N (%)	Red	0.04 (0.01)	−7.90	<**0.001**
	Black	0.13 (0.01)		

significant, but suggestive growth difference with an average of 57% less biomass when grown in red soil (Fig. 3A).

Multiple linear regressions yielded significant relationships between shoot biomass and soil nutrients for the non-native plant species. In contrast, no significant relationships were evident between native plant shoot biomass and soil nutrients, with the exception of *Ceanothus*. Multiple regression equations are presented in Table 6.

4.4. AM fungal colonization

Paired t-tests indicated percent root colonization by AM fungi for each plant species was highly variable, but, on average, less in plants grown in red soil regardless of whether the plant was native or non-native (Fig. 3B). Non-native plants, *Centaurea*, *Brachypodium*, and *Bromus*, had 98%, 87%, and 79% less AM fungal colonization, respectively, when grown in red soil. Native plants, *Elymus* and *Epilobium*, had 61% and 98% less AM fungal colonization, respectively, when grown in red soil. *Ceanothus* showed no indication of colonization by AM fungi, but did form dense root hairs not found in other plant species in this study. This variable, but typically lower AM fungal colonization in red soil compared to black soil, is likely attributed to the death of these symbiotic microorganisms when the upper organic layers are consumed during high-severity fire (Neary et al., 2005).

4.5. Vegetation survey

Sixteen plant species were identified on the 20 paired 1 m^2 permanent plots. Of those species, only 3 (*C. velutinus*, *E. angustifolium*, and *R. ursinus*) had constancy >0.4. The percent vegetative cover 2 yrs post-fire was significantly lower ($P < 0.05$), with 51% less vegetative cover, on red soil plots than black soil plots (Table 7).

5. Discussion

5.1. Comparing severely burned soil

Few studies have examined variable soil burn severity as a factor in the establishment and growth of native and non-native plant species. Our study is unique in that we investigated the

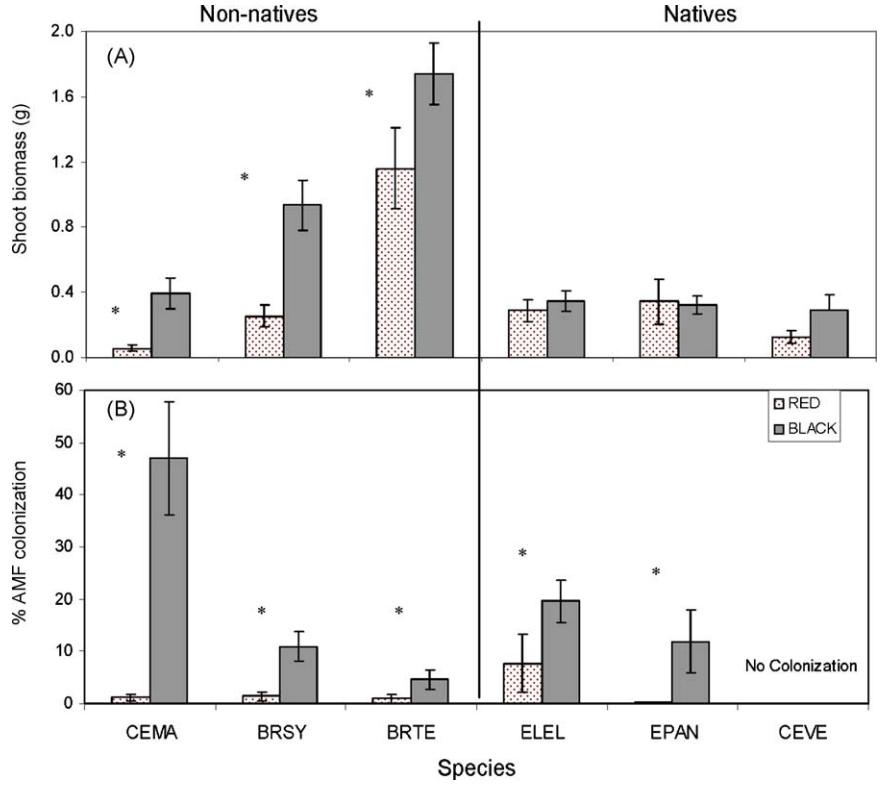

Fig. 3. (A) Shoot biomass of the 3 native and 3 non-native plant species grown in the growth chamber. (B) AM fungal root colonization of the 3 native and 3 non-native plant species grown in the growth chamber. CEMA (*Centaurea maculosa*); BRSY (*Brachypodium sylvaticum*); BRTE (*Bromus tectorum*); ELEL (*Elymus elymoides*); EPAN (*Epilobium angustifolium*); CEVE (*Ceanothus velutinus*). Error bars represent SEM. Significant differences between means ($\alpha = 0.05$) are denoted with an (*).

Table 6
Multiple linear regression models of the response variable plant shoot biomass grown in red or black soil and soil chemical variables resulting from manual backwards selection. SE denoted in parentheses ($n = 20$). Bolded text indicates statistical significance ($\alpha = 0.05$).

	Species	Equation	R^2
Non-natives	CEMA	$=-0.4\ (0.1) + 0.3\ (0.1) \times \text{severity} - 0.003\ (0.001) \times NH_4 + 0.2\ (0.05) \times C + 0.02\ (0.006) \times P$	**0.85**
	BRSY	$=-0.2\ (0.2) - 0.002\ (0.1) \times \text{severity} + 0.006\ (0.002) \times NH_4 + 0.2\ (0.08) \times C$	**0.85**
	BRTE	$=0.007\ (0.3) - 0.2\ (0.3) \times \text{severity} + 0.009\ (0.003) \times NH_4 + 0.7\ (0.1) \times C + 0.4\ (0.1) \times \text{severity:C}$	**0.83**
Natives	ELEL	$=0.3\ (0.07) - 0.06\ (0.09) \times \text{severity}$	0.02
	EPAN	$=0.3\ (0.1) + 0.06\ (0.1) \times \text{severity}$	0.01
	CEVE	$=-0.008\ (0.08) - 0.14\ (0.1) \times \text{severity} + 0.1\ (0.02) \times C - 0.009\ (0.002) \times P + 0.06\ (0.02) \times \text{severity:P}$	**0.84**

chemistry, microbial communities and plant growth in naturally occurring severely burned red soils, which smoldered much hotter and longer than comparable soil conditions assessed in other studies. Severely burned soil found inside slash pile scars did not show the extreme limitation of nutrients found in red soils examined in our study. For example, Korb et al. (2004) investigated the effects of slash pile burning on soil biotic and chemical properties. They reported an 18%, 20%, and 9% reduction in soil C, N, and P, respectively, inside severely burned slash pile scars from the unburned soil outside the scar. In comparison, the severely burned red soil examined in our study contained 71%, 69%, and 71% less total soil C and N, and less plant available P, respectively, than the less severely burned black soil.

In the event of wildfire, increased fuel loads have the potential to increase the area of severely burned red soil thought to be more susceptible to colonization by weedy plant species (Brown et al., 2003). Furthermore, high densities of fire-killed trees after a severe wildfire may increase the area of red soil in the event of a reburn (Poff, 1989; Brown et al., 2003; Shank, 2004; Monsanto and Agee, 2008). Therefore, knowledge of the impact of severe surface burning on soil nutrients, soil microbial communities and post-fire plant re-colonization is critical to forest recovery projects (Busse et al., 2007).

Table 7
Percent vegetative cover on meter^2 burn severity plots at each site. Bolded text denotes a significant difference between means ($P < 0.05$, $n = 10$).

Site	Severity	% Cover
UJ-1	Red	28
	Black	78
UJ-5	Red	21
	Black	65
LJ-7	Red	19
	Black	25
LJ-10	Red	35
	Black	85
LJ-12	Red	25
	Black	53
BH-1	Red	18
	Black	35
BH-6	Red	13
	Black	28
1210-3	Red	23
	Black	48
1210-6	Red	27
	Black	43
1280	Red	38
	Black	50
Mean (SE)	Red	**24.7** (2.4)
	Black	**51.0** (6.3)

5.2. Factors influencing shoot growth

In our study, the opportunistic non-native plants grew more rapidly than native plants, although the shoot biomass of non-native plants grown in red soil was significantly less than the same plants grown in black soil. In contrast, growth responses of pioneering native plant species were similar, regardless of burn severity, AM fungal colonization, or plant type (e.g., grass, forb, woody shrub) (Fig. 3A). These findings suggest that some native species may outperform invasive species in low-resource environments, such as severely burned red soil, an alternative hypothesis to the evidence presented by Funk and Vitousek (2007).

Even though AM fungi are important to plant establishment and growth (Smith and Read, 2008), the growth of plants in our study was not affected by the abundance of mycorrhizal symbionts in their roots. Percent colonization of AM fungi did not explain why non-native plants had significant differences in biomass when grown in soil from different burn severities, while native plants did not. We did find, however, that colonization by AM fungi in all plant species, with the exception of the native *Ceanothus*, was lowest in plants grown in red soil, regardless of whether the plant was native or non-native (Fig. 3B). This finding supports the hypothesis by Hart et al. (2005) that fires burning through heavy fuel loads (thus increasing burn severity) are likely to lead to much larger reductions in AM propagules than lower intensity fires. Similarly, fire does not uniformly heat the soil, so the variability in AM fungal colonization found in red soils could be attributed to the variable fuel loads influencing soil burn severity.

Although AM fungal colonization did not account for the differences in growth between native and non-native species, multiple linear regressions revealed that non-native plant species showed strong correlations with soil nutrient availability, while native plants did not (except for the N-fixing shrub, *Ceanothus*) (Table 6). These results suggest that, for the limited growth period of our study, soil nutrient availability was more influential to plant growth than AM fungal partnerships. Future studies with a nutrient amendment component, as well as determining the nutrient content of plants, may provide further evidence of a nutrient mechanism.

The differential response of native and non-native plant species to soil nutrient availability could be explained by a theory proposed by Davis et al. (2000), based on Grime's triangular model of plant strategies (Grime, 1974). This theory proposes that plant communities become more susceptible to invasion with increased amounts of unused resources. The theory describes how disturbances, such as fire, increase the amount of unused resources of an area by reducing the rate of resource capture by the native vegetation, thus heightening the invasibility of that area. Although increased invasion in response to resource availability has not been demonstrated for all invasive species (LeJeune et al., 2006), many invasive species tend to be R-selected ruderals associated with short life spans and high seed production, having evolved in severely disturbed but potentially productive environments (Grime, 1977). In our study, all three of the invasive species

chosen were R-selected ruderals. We observed increased biomass in these species compared to the native plant species and strong correlations between invasive species and soil nutrient availability. These results therefore support the theory by Davis et al. (2000) of invasive plant resource exploitation.

5.3. Soil microbial community structure through PLFA analysis

Soil burn severity was the most important factor influencing microbial community structure in our study. Results from PLFA analyses showed that the soil microbial communities of severely burned red soil differed from moderately burned black soil both in freshly collected soil and in soil collected after 10 weeks of plant growth. Severe soil heating as well as loss of organic matter increased the mortality of all soil microbial groups in red soils. Except for AM fungi and protozoa, relative abundance (mol %) of most microbial groups in freshly collected soil was lowest in red soils (Table 3). This finding was unexpected because fungal and protozoan groups are sensitive to soil heating (Hart et al., 2005). This observation may be attributed to soil from site LJ-10 having disproportionately high PLFA signatures for AM fungi and protozoan groups, although no other biological or chemical reason was found to disregard this site.

5.4. Vegetation recovery

Our findings indicate that burn severity influences microbial dynamics and soil nutrient availability; each of these factors affects plant initiation and development in burned areas. Vegetation surveys 2 yrs post-fire revealed that percent cover was more than 50% lower on red soil in all plots (Table 7). Net mineralizable N and available soil P were substantially reduced in red soil by 73% and 71%, respectively (Table 5), possibly contributing to the lower percent cover observed on these soils. Other researchers have described the decrease in plant biomass with increasing burn severity for up to 2 yrs post-fire (Feller, 2000). Our observations support the hypothesis that red soils will have slower vegetative recolonization because high-severity fire degrades more of the plant seed bank and AM fungal propagules, in addition to altering soil nutrient and water availability, thus affecting the post-fire community (Rowe, 1983).

Several plant species, including *C. velutinus*, *E. angustifolium*, and *R. ursinus*, were present in relatively high abundance (constancy >0.4) on red soil plots. High-severity fire can consume the entire organic horizon and seeds of most plant species (Whittle et al., 1997), but some shrub species, such as *C. velutinus* (Conard et al., 1985), and herbaceous plants, such as *E. angustifolium* (Feller, 2000) are promoted by soil heating (Christensen and Muller, 1975) and have been documented to increase with burn severity (Schimel and Granstrom, 1996). Thus, conditions created by high-severity fire or slash burning may improve the establishment of these species (Whittle et al., 1997).

No non-native plants were present on our plots up to 2 yrs after the fire. Invasive species may have been lacking before the fire and hence, post-fire presence was limited by seed source. Although it is possible that non-native species could become established in the future, uncertainty is high because colonization at a specific location is affected by many factors in addition to soil biota, including competition, propagule production, and seed dispersal (Levine et al., 2004). Because individual plant species react differently to soil biota in various ecosystem types, it is important not to generalize about which variables influence non-native plant species invasion. Future research is needed to investigate how individual plant species respond to these variables in different ecosystems.

6. Conclusions

Red soil conditions caused by severe soil heating alter soil nutrients and microbial community structure compared to less severely burned black soils. Our study revealed that red soils were highly nutrient-limited and exhibited reduced microbial abundance, AM fungal propagules and plant growth. Our results suggest that although burned soils in general promote growth of non-native invasive plants, these species may be less competitive in severely burned sites where organic matter, soil nutrients, and microbes are reduced due to severe soil heating. Our findings demonstrate the importance of plant, soil nutrient, and soil microbe interactions as determinants of plant community structure and diversity. Other factors not investigated in this study, such as dispersal, propagule production, competition with resident plant species, fire feedbacks and interactions with other biota, likely also influence the success of non-native invasive plants after high-severity fire. With the potential for red soils to comprise a substantial area of land if large amounts of large down wood are present before fire, it is important to continue to monitor red soil sites to further our understanding of the impacts of severely burned soil on post-fire ecosystem recovery.

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